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Changes in microbial communities along redox gradients in polygonized Arctic wet tundra soils

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Summary

This study investigated how microbial community structure and diversity varied with depth and topography in ice wedge polygons of wet tundra of the Arctic Coastal Plain in northern Alaska and what soil variables explain these patterns. We observed strong changes in community structure and diversity with depth, and more subtle changes between areas of high and low topography, with the largest differences apparent near the soil surface. These patterns are most strongly correlated with redox gradients (measured using the ratio of reduced Fe to total Fe in acid extracts as a proxy): conditions grew more reducing with depth and were most oxidized in shallow regions of polygon rims. Organic matter and pH also changed with depth and topography but were less effective predictors of the microbial community structure and relative abundance of specific taxa. Of all other measured variables, lactic acid concentration was the best, in combination with redox, for describing the microbial community. We conclude that redox conditions are the dominant force in shaping microbial communities in this landscape. Oxygen and other electron acceptors allowed for the greatest diversity of microbes: at depth the community was reduced to a simpler core of anaerobes, dominated by fermenters (*Bacteroidetes* and *Firmicutes*).

Introduction

A major challenge in microbial ecology is identifying what environmental controls shape the complex communities found in soils. The difficulty in predicting the abundance and distribution of microbial species in soils stems from the overwhelming complexity of the communities and our ignorance of the natural history of most of these species. Several studies show that pH is important for predicting community structure on large spatial scales (Fierer and Jackson, 2006; Chu *et al*., 2010; De Vries *et al*., 2012), and numerous studies have linked variations in microbial community structure with other soil characteristics, such as organic matter and nutrient content, texture and soil structure, and with vegetation patterns (Högberg *et al*., 2007; Merilä *et al*., 2010; Smith *et al*., 2010; Chau *et al*., 2011; Ganzert *et al*., 2011; Zinger *et al*., 2011; Brockett *et al*., 2012; Kuramae *et al*., 2012; Hu *et al*., 2014). Less is known about controls over spatial variation in communities at smaller scales, which can rival that at larger scales (Eilers *et al*., 2012; Vos *et al*., 2013).

In the light of climate change, understanding spatial variability in Arctic ecosystems is particularly critical. The potential impacts of climate change on arctic ecosystems and microbial communities are a major concern, as the Arctic is warming rapidly and microbial communities control C cycle feedbacks that could accelerate global warming by release of greenhouse gases from C (and potentially N) stored in the permafrost (Schaefer *et al*., 2014). Efforts to model the responses of this ecosystem to climate change are hampered by high site-to-site variability, driven mainly by hydrological patterns (Zona *et al*., 2010; McGuire *et al*., 2012; Sturtevant and Oechel, 2013).

Chu and colleagues (2010) concluded that surface Arctic soil microbial communities were not fundamentally different from those of other ecosystems, and found that pH accounted for most of the large-scale spatial variation in these microbial communities across hundreds of kilometres. The sites chosen for that study were well-drained, upland dry heath tundra soils, whereas the current study focuses on fine-scale variation in high Arctic wet tundra soils. Soils of wet sedge Arctic tundra ecosystems are unique in that they are underlain by permafrost, blocking drainage and leading to anoxic or suboxic conditions through much of the soil profile. Ice wedges form as melt water fills into cracks from repeated freeze-thaw cycles, pushing up areas of soil and creating ice wedge polygons, generally about 30 m in diameter. Ice wedge polygon formation leads to topographic variation in these landscapes, creating higher, drier areas and lower, wetter

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areas within meters of each other (Brown, 1967) (Fig. S1). Water table depth and topography strongly control biogeochemical cycling in this ecosystem (Zona *et al.*, 2011; 2012; Lipson *et al.*, 2012), and a metagenomic analysis of soils in this ecosystem showed changes in the relative abundance of metabolic pathways through a depth profile, with anaerobic pathways generally increasing with depth (Lipson *et al.*, 2013a). However, the structures of the soil microbial community in this ecosystem and the factors that control its variation over small spatial scales have not been described in great detail. Furthermore, despite the central importance of redox chemistry to biology, redox potential is generally neglected in studies that attempt to explain the composition of soil microbial communities.

This study presents an extensive 16S rRNA gene dataset, with over two million sequences, produced from varying depths (6–10 cm, 16–20 cm, 26–30 cm and 36–40 cm) of replicate soil cores from rims and centres of low-centered polygons, representing areas of high and low topography respectively. These features were sampled from six drained thaw lake basins, which form a major part of the landscape in the Arctic Coastal Plain near Barrow, Alaska (Hinkel *et al.*, 2005). Soil chemistry data are used to infer the driving forces that structure soil microbial communities in this ecosystem.

Results and discussion

Soil chemistry

Soil properties varied significantly with depth (Fig. 1). Total soil organic matter and dissolved organic C decreased with depth, as the soils transitioned from organic to mineral layers. More reducing conditions were found in deep layers of the soils, as shown by the increased ratio of reduced iron [Fe(II)] to total Fe (Fe2/tot) in acid extracts. Consistent with this pattern, pH also increased slightly with depth as protons are consumed by anaerobic processes such as Fe(III) reduction (Lipson *et al.*, 2012). The effect of ice wedge polygon-driven topography (i.e. high versus low) was generally more subtle but can be seen in the levels of nitrate and lactate in soil water extracts (Fig. 1E and F). Nitrate is generally found at low concentrations in these predominantly suboxic soils (Lipson *et al.*, 2010; 2012), but is sporadically found at higher concentrations in the more oxic, raised areas of polygon rims (Fig. 1E). Conversely, the

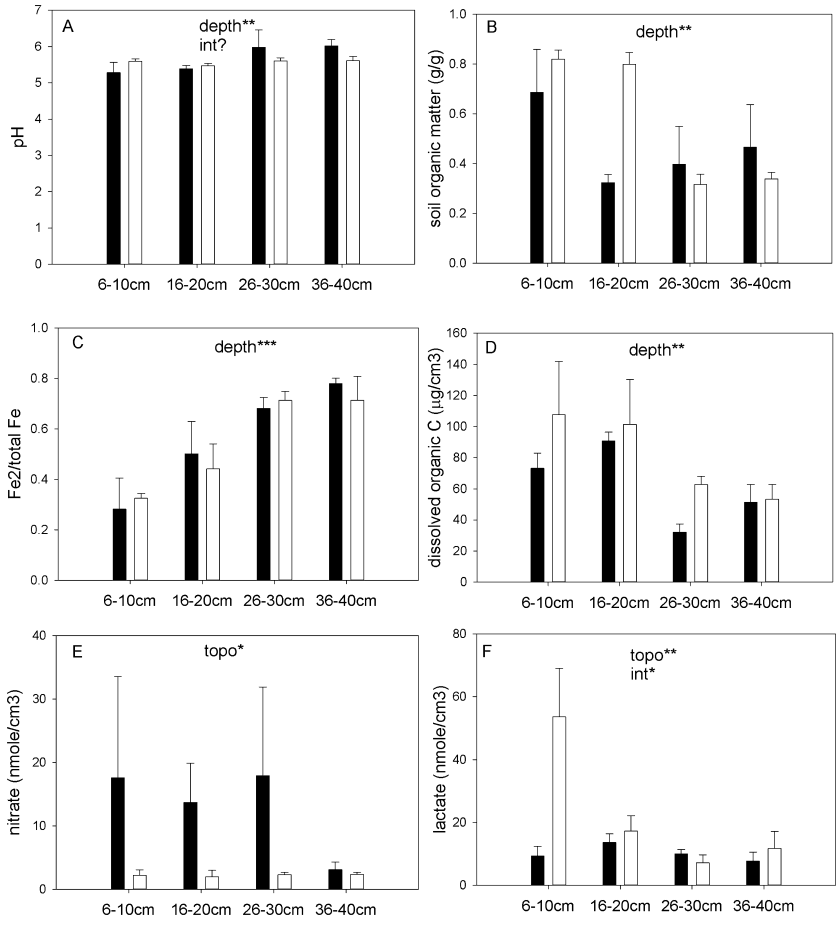

Fig. 1. Soil properties by topography and depth. Values are means with standard errors. Topography (topo): black bars = polygon rims, white bars = polygon centres. Significance in analyses of covariance: ***significant at $P < 0.001$, **$P < 0.01$, *$P < 0.05$, ?$P < 0.1$; int = topo × depth interaction. Soil ph was measured in water saturation paste and soil organic matter content by loss on combustion at 500°C. Oxidized and reduced forms of iron in acid extracts (1M HCl) were analysed using 1,10-phenanthroline (Lipson *et al.*, 2010). Water extracts were analysed for total dissolved organic carbon with a colorimetric method (Lipson *et al.*, 2010) and for nitrate and lactate by ion chromatography, using a Thermo Dionex ICS 5000+.

fermentation product lactate was found at low concentrations in shallow regions of rims compared with the lower, wetter, more anoxic polygon centres. Different forms of organic acids (OA) showed distinct patterns with depth and topography (Table S1): for example, formate increased with depth while citrate decreased with depth; acetate was highest in shallow layers of polygon rims. The effects of topography on OA and nitrate were most pronounced in shallow layers, which is to be expected as these layers emerge above the water table in these landscapes. Different redox couples dominate over the range of redox states (for example NO_3^- is reduced at more positive potentials than Fe^{2+}), and so it is not surprising that multiple soil chemistry variables (e.g. Fe2/tot and OA) are required to capture the full range of redox states in this ecosystem.

Overall community structure

A principal component analysis (PCA) using weighted UniFrac distances shows that microbial community structure is strongly controlled by depth in the soil profile (Fig. 2). Three PCs accounted for 68% of microbial community variation among samples (49.4, 11.7 and 7.1% respectively). Samples from the same depth tend to cluster together when plotted by their first two PC scores. In a multivariate analysis of variance (MANOVA), the three PCs were significantly affected by both depth (Pillai's trace, $P < 0.001$) and topography ($P = 0.004$). The effect of topography seems to be driven by the upper layers: among 6–10 cm samples, polygons rims and low centres form distinct clusters. Also, 16–20 cm samples from rims tend to group with 6–10 cm samples from centres. Because of the offset in altitude, these samples may have similar water table depths and hence, similar communities. However, the depth × topography interaction was only marginally significant in the MANOVA ($P = 0.059$).

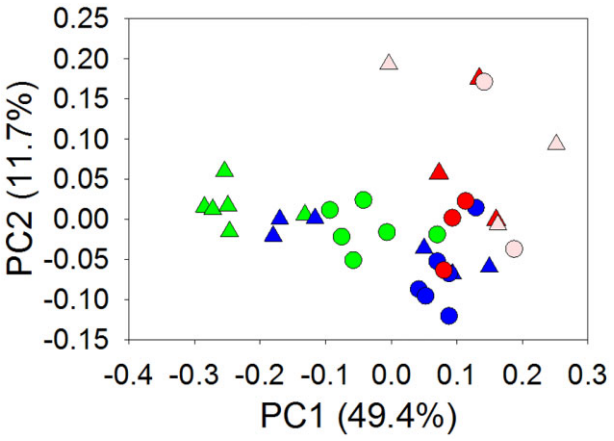

Fig. 2. Principle component analysis of variation in microbial community structure by topography and depth. The percentage of total variation in weighted UniFrac distance among samples explained by the first two principle components is shown in parentheses. Topography is indicated by shape (triangles = polygon rims, circles = polygon centres) and depth is indicated by colour (green = 6–10 cm, blue = 16–20 cm, red = 26–30 cm and pink = 36–40 cm).

The variations in microbial community structure with depth and topography on the community are consistent with what has been reported for this ecosystem. Topography and water table depth, and hence redox status, control biogeochemical cycling in this and other Arctic tundra ecosystems (Wagner *et al.*, 2003; Sommerkorn, 2008; Lipson *et al.*, 2012). Metagenomic analysis along a depth profile in this ecosystem showed that aerobic metabolic genes decline while anaerobic pathways increase with depth (Lipson *et al.*, 2013a), and the prevalence of anaerobes in permafrost has been noted in several studies (Jansson and Tas, 2014).

The two deepest layers (26–30 and 36–40 cm) are not distinguishable from each other in this analysis (Fig. 2). The active layer thickness in these landscape features (drained thaw lake basins) are typically in the range of 26–36 cm (Shiklomanov *et al.*, 2010), and so the 26–30 cm samples generally represent the lower active layer and the 36–40 cm samples, the upper permafrost or, given its variable nature, the transition zone (Shur *et al.*, 2005). Active layer depth varies over the landscape and from year to year (Shiklomanov *et al.*, 2010; Lipson *et al.*, 2013b), and given that biological activity continues well below the bulk freezing point of water (Panikov, 2009), this somewhat fuzzy boundary may not represent a major qualitative shift in the environment for soil microbes, but rather a quantitative one. Presumably there is more microbial activity in the lower active layer, which reaches a maximum temperature of about 2°C versus just below 0°C in the upper permafrost (Hinkel *et al.*, 2001). For example, increased microbial activity was observed with increased active layer thickness in a landscape-level flooding experiment (Lipson *et al.*, 2012; Zona *et al.*, 2012). Studies in the discontinuous permafrost zone of interior Alaska showed strong microbial community responses to permafrost melting (Mackelprang *et al.*, 2011; Hultman *et al.*, 2015). While increases in active layer depth in areas of continuous permafrost could have large impacts through C cycle-climate feedbacks (Hollesen *et al.*, 2011; Koven *et al.*, 2011; MacDougall *et al.*, 2012; Schaefer *et al.*, 2014), they are unlikely to produce major shifts in microbial communities at the high Arctic sites of the present study.

Both depth and topography strongly influenced diversity (Fig. 3). Estimated operational taxonomic unit richness (controlling for number of sequences, see Table S2) declined with depth in the soil profile, with diversity in the surface layer almost twice that of the deepest layer. Similarly, polygon rims were more diverse than centres. The

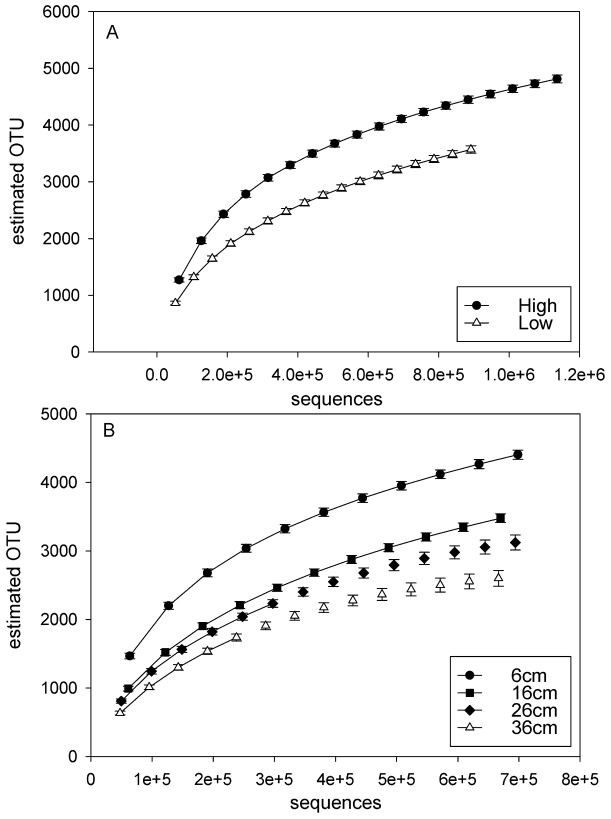

Fig. 3. Rarefaction curves on combined samples by topography and depth. High = polygon rims, Low = polygon centres. Symbols without lines represent extrapolated values. Operational taxonomic unites were defined at 97% identity, and rarefaction analysis was done with estimates (Colwell *et al*., 2012).

results were similar when samples were analysed individually: mean Chao1 values declined significantly with depth and in polygon centres (Table S3).

The decrease in diversity under more reducing (deeper and/or wetter) conditions probably represented not just lower levels of oxygen but also a general loss of alternative electron acceptors. Oxygen declines rapidly below the water table and is generally anoxic by 5–10 cm below the soil surface (Lipson *et al*., 2010; 2012). However, the decline in diversity was more or less continuous throughout the entire profile, continuing to decline well after oxygen would have dropped to very low levels. Iron oxide is a major alternative electron acceptor for anaerobic respiration in these soils (Lipson *et al*., 2013b), and as Fig. 1C shows, the availability of iron oxide declines with depth. Therefore it seems that oxygen and other terminal electron acceptors allowed for the greatest diversity of microbes: in their absence the community is reduced to a simpler core of anaerobes, dominated by fermenters. The *Firmicutes* sequences in this study, which were found in much greater abundance at depth, consisted almost entirely (92%) of the predominantly fermentative *Clostridiales*. Similarly, the *Bacteroidetes* sequences were dominated (86%) by the generally fermentative *Bacteroidales*. A recent study conducted about 850 km south in shrub and tussock-dominated upland tundra sites near Healy, Alaska found similar trends in diversity and community structure with depth, though these authors did not report a measure of redox potential and mainly attributed these patterns to changes in pH and C availability (Deng *et al*., 2014). Microbial biomass tends to decline with depth in soil profiles (Eilers *et al*., 2012), and so a decrease in diversity with depth is consistent with the general relationship between diversity and numbers of individuals classically observed in ecology (MacArthur, 1967). Decreased diversity was observed with depth in a marine oxygen minimum zone, and this was interpreted as fitting predictions of diversity–energy theory, in which reduced energy availability leads to reduced diversity (Bryant *et al*., 2012).

Patterns of taxa with depth and topography

The relative abundance of sequences from individual taxa and functional groups (inferred from phylogeny) also show clear responses to depth and topography (Fig. S2). Taxa associated with anaerobic functions, methanogenic *Archaea* and iron-reducing *Geobacteraceae*, declined in the more oxic polygon rims relative to low polygon centres. Conversely, sequences of the aerobic iron-oxidizing *Gallionelliaceae* were more abundant in rims. The majority of sequences associated with aerobic methylotrophic taxa were facultative methylotrophic *Betaproteobacteria*. These sequences and those belonging to the obligate type I and II methanotrophs declined with depth (Fig. S2D and E). Similarly, sequences related to the acidophilic methane oxidizing *Verrucomicrobia* genus, *Methylacidiphilum*, were most abundant in shallow regions of rims and declined with depth and in low centres (Fig. S2F). Sequences related to anaerobic methane oxidizers tended to follow opposite patterns: the NC10 phylum, associated with nitrite-dependent methane oxidation (Ettwig *et al*., 2009), was marginally more abundant in polygon centres and the *Methanosarcinales* order, which contains the anaerobic methane-oxidizing *Euryarcheota* group ANME 2 (Knittel *et al*., 2005), was more abundant in polygon centres and increased with depth.

Most major taxa analysed at the phylum or class level varied significantly with depth and/or topography (Fig. S3). The shallow layer is enriched in *Acidobacteria* and *Alphaproteobacteria*, while the deepest layer is dominated by *Bacteroidetes, Actinobacteria* and *Firmicutes*. In addition to the more abundant taxa shown in Fig. S3, some relatively rare taxa varied with depth (*Caldiserica, Elusimicrobia*), topography (*Gemmatimonadetes*) or to both factors (*Gammaproteobacteria, Planctomycetes, Crenarchaeota*). The spatial distribution of the diverse and

abundant *Betaproteobacteria* only showed marginally significant trends, but when separated into its major families, relationships become apparent (Table S4). For example, *Burkholderiaceae* declined sharply with depth while *Comamonadaceae* increased.

In the aforementioned analyses, depth was treated as a continuous variable, and so only linear effects were considered. When depth was coded as a categorical variable, the nonlinear depth pattern (maximum at 16–20 cm) of *Deltaprotebacteria* (Fig. S2G) was highly significant ($P < 0.0001$).

Explaining microbial patterns with soil chemistry

The spatial patterns in microbial community structure were explained well by patterns in soil chemistry. Fe2/tot indicates the redox status of the samples, and was the best predictor of overall community structure, as represented by PCA (Table 1). Fe2/tot explained 61.4% of the variation in the three PCs, mainly through relationships with PC1 and PC2. Soil pH was not as good of an overall predictor, explaining only 42.4% of the variation. Dissolved organic carbon (DOC) helped explain PC2 and PC3. Lactate was the best predictor among the OA or other chemical species. Total OA and lactate mainly explained variation in PC3. Total soil organic matter (OM) was not significant in this analysis ($R^2 = 0.177$).

It is surprising that soil OM was a poor predictor of the microbial community, as this variable indicates not just the total amount of carbon potentially available to microbes, but also signals the transition from the upper organic layers to the lower mineral layers, and therefore a major change in texture (Bockheim *et al*., 2001). This sharp organic-to-mineral transition was apparently less critical than the continuous decline in redox state with depth. This is in contrast to results found by Tas and colleagues (2014), who found that, in addition to depth, the organic to mineral transition was a key factor in controlling microbial community structure and diversity in a boreal forest soil profile. The discrepancy between these two studies may be due to cryoturbation, which mixes soil layers in Arctic soils and could make the transition between layers less sharp (Bockheim, 2007).

The above analysis compared individual variables as predictors of microbial community structure. To see how well combinations of these variables predicted the three PCs, we used MANOVA (Table S5). This analysis showed that Fe2/tot and lactate together were the best predictors of community structure. When controlling for Fe2/tot, lactate was highly significant ($P = 0.005$), total OA was significant ($P = 0.039$), acetate was marginal ($P = 0.054$) and other OA (citrate, oxalate, formate) were not significant. When controlling for Fe2/tot, pH and OM were not significant and DOC was marginal ($P = 0.098$).

Lactate complemented Fe2/tot as an explanatory variable because it was the best predictor of several groups that were not explained well by Fe2/tot, such as the facultative methylotrophs (mainly *Betaproteobacteria*), *Geobacteraceae* (Fe reducers), methanotrophic *Archaea* and others (Table S6). These groups had complex patterns with depth and topography. Lactate could be linked many possible ways to these groups, both directly and indirectly. For example, lactate is an energy source for some *Geobacter* species (Call and Logan, 2011), which can transfer electrons to methanogens for syntrophic growth (Rotaru *et al*., 2014).

Predicting the abundance of specific taxa with soil chemistry

The relative abundance of individual taxa was also best predicted by redox status, as indicated by Fe2/tot. Correlation analysis (Table S6) showed that this variable was the best predictor in all cases where a soil variable was significant except for *Firmicutes* (pH, $r = 0.729$; Fe2/tot, $r = 0.675$), *Verrucomicrobia* (pH, $r = –0.475$; Fe2/tot, $r = –0.405$) and *Hydrogenophilaceae* (OM, $r = –0.565$; pH, $r = 0.384$; Fe2/tot, $r = 0.358$; DOC, $r = –0.374$).

As was the case for overall microbial community structure, lactate concentration was highly correlated with several microbial groups, including facultative methylotrophs ($r = 0.739$; $P < 0.0001$), Fe reducers ($r = 0.567$, $P = 0.006$) and *Burkholderia* ($r = 0.587$, $P = 0.004$).

Table 1. Results of multiple regression analysis of soil variables on the three principal components describing variation in microbial community structure. Principal component analysis using the weighted UniFrac metric (Lozupone *et al*., 2006) was generated by QIIME (Caporaso *et al*., 2010). Multiple regression analysis was used to relate soil chemistry variables to individual PC.

	PC1		PC2		PC3		Overall		
Variable	*t*	*P*	t	*P*	*t*	*P*	R^2	*F*	*P*
Fe2/tot	4.63	0.0002	2.31	0.032	–0.59	0.563	0.614	10.09	0.0003
pH	2.61	0.0174	2.31	0.032	–0.23	0.820	0.424	4.66	0.0133
DOC	–1.03	0.3178	–2.22	0.039	2.51	0.022	0.383	3.94	0.0243
OA	–0.06	0.9564	–1.76	0.094	2.36	0.029	0.293	2.62	0.0807
Lactate	–0.29	0.7785	–1.04	0.314	3.62	0.002	0.433	4.59	0.0149

The strong correlations of overall microbial community structure and the relative abundance of individual taxa with depth, topography and redox status highlight the importance of redox in structuring microbial communities in this ecosystem. While some studies have addressed this effect in soils (DeAngelis *et al*., 2010; Liang *et al*., 2012), far more attention has been given to pH (Fierer and Jackson, 2006; Chu *et al*., 2010; De Vries *et al*., 2012), vegetation (Chu *et al*., 2011; Fierer *et al*., 2011; Lamb *et al*., 2011; Legay *et al*., 2014), OM content and quality (including C:N ratio) (Högberg *et al*., 2007; Merilä *et al*., 2010; Nemergut *et al*., 2010; Ganzert *et al*., 2011; Zinger *et al*., 2011; Kuramae *et al*., 2012; Tas *et al*., 2014), water content (Smith *et al*., 2010; Brockett *et al*., 2012) and texture/structure (Carson *et al*., 2010; Chau *et al*., 2011; Hu *et al*., 2014) as potential explanatory variables for variations in soil microbial communities. Given the high organic content of the peat soils in this study, microbes may not generally experience C limitation (Allen *et al*., 2009; Von Fischer *et al*., 2010), and so limitation by other factors, such as electron acceptor availability, would naturally be a stronger force in structuring these communities. Nobel laureate, Albert Szent-Gyorgi is quoted as saying 'Life is an electron looking for a place to rest' (Trefil *et al*., 2009), and as Husson (2013) noted, pH is often viewed as a master variable while Eh (redox potential) is neglected, despite the fact that biology relies far more on oxidation–reduction reactions than acid–base reactions.

In conclusion, this study gives insight into how environmental factors structure microbial communities on small spatial scales, ranging from depth gradients on the order of 30 cm to variation across ice wedge polygons on the order of 30 m, and shows the overriding effect of redox on community composition and diversity in polygonized wet tundra soils. Since redox status can generally be predicted from water table depth, which in turn can be predicted from elevation in this landscape (Liljedahl, 2011), these results could provide the basis for spatially explicit modelling of microbial communities across the landscape in this region. It also provides a description of the microbial community that is unprecedented in its sequencing depth for this ecosystem.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Fig. S1. Image of low-centered polygons (dark, wet areas) rimmed by higher, drier areas pushed up by ice wedges (photo: D. Lipson).
Fig. S2. Relative abundance of major taxa by topography and depth. Values are means and standard errors. Topography (topo): black bars = polygon rims, white bars = centres. Significance of analysis of covariance (ANCOVA): ***significant at $P < 0.001$, **$P < 0.01$, *$P < 0.05$, ? = $P < 0.1$; int = topo × depth interaction
Fig. S3. Relative abundance of functional groups by topography and depth. Values are means and standard errors. Topography (topo): black bars = polygon rims, white bars = centres. Significance of ANCOVA: *** = significant at $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, ? = $P < 0.1$; int = topo × depth interaction. See main text for interpretation of function.
Table S1. Total (μg C cm^{-3}) and individual (nmole cm^{-3}) organic acids (means and standard errors) in water extracts of soils from varying depths of rims or centres of low-centered polygons.
Table S2. Sequencing effort for soil samples of different depths (in cm) and topography (high and low are rims and centres, respectively, of low-centered polygons). Operational taxonomic units were determined by two alternative clustering algorithms, UCLUST and UPARSE.
Table S3. Means (and standard errors) of sequences per sample, unique OTU per sample and the Chao1 estimate of OTU richness for topographically high and low areas and different depths, using two different clustering methods to assign sequences to OTU. ANOVA results: Chao1 by UCLUST: high versus low ($P = 0.001$), depth ($P < 0.001$); Chao1 by UPARSE: high versus low ($P = 0.038$), depth ($P < 0.001$).

Table S4. Percentage of major families (*Burkholderiaceae, Comamonadaceae, Gallionellaceae, Methylophilaceae, Rhodocyclaceae*) within the *Betaproteobacteria* by topography and depth (Int = depth × topography interaction)

Table S5. Multivariate analysis of variance of the three principle components describing variation in microbial community (weighted UniFrac) on combinations of soil variables. Pillai = Pillai's trace, dfe = degrees of freedom (error), Fe2/tot = reduced Fe over total Fe in acid extracts (a measure of redox), DOC = dissolved organic carbon, OA = organic acids, OM = organic matter.

Table S6. Correlation coefficients between taxa abundance and soil chemical parameters. Significance is colour coded: pink text, white background, $P < 0.1$; pink background, $P < 0.05$; yellow, $P < 0.01$; green, $P < .001$ (OM = organic matter, DOC = dissolved organic C, OA = organic acids, PO_4 = phosphate, Cl^- = chloride, Br^- = bromide, FeR = Fe reducers, Methano = methanogens, Methylo = methylotrophs).